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THE METAMORPHOSIS OF FLIES.* II.

BY DR. AUGUSTUS WEISSMANN.

WE now attempt to consider morphologically the phenomena of the development of the Muscidæ, as discussed in the foregoing chapters. In the first place, the theories above laid down seem to be thoroughly established, *i. e.* that we have in the metamorphosis of the flies nothing to do with a simple change of skin. Indeed, the additional metamorphosis is accompanied by a casting aside and new formation of the chitinous framework which underlies the body, but this has a very subordinate signification. The systems of organs of the larva disappear simultaneously, it may be completely, it may be only histologically; and out of the fragments the tissues build up a new body. It is a matter of doubt whether to consider the larva and pupa as one and the same individual, or whether we have not in reality an alternation of generations. I think that those who speak of a metagenesis in certain Echinoderms should regard this also as such, if with V. Carus,† we consider metamorphosis as a series of developments in which the animal, during a certain stage in its development, is provided with provisional organs; but metagenesis as that in which this whole developmental stage itself (Amme) must be considered as a provisional one, so that it readily follows that the system of organs of the larva taken collectively is provisional, or in other words, that the larva itself is a provisional stage, while the fly must be considered as a new individual; such process taking rank as an alternation of generations. At all events from the Pluteus-form larva new organs arise in the sea star, as from the larva in the fly. There is the alimentary canal and the water vascular system, which last, though in a plainly undeveloped condition, is already partially developed in the larva. Here we have, except the hypoderm of the abdominal segments of the larva, no parts which pass into the pupa without previously undergoing a total revolution. The alimentary canal and the water-vascular system of the Echinoderm larva at no time perform their function; they continue to develop more perfectly; they grow more complicated in their structure; they throw off their parts singly; they only hold in reserve their histological structure in order to become physiologically capable of performing their functions.

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*Forming the closing chapter in "Die Entwicklung der Dipteren," 1864.

†System der thierischen Morphologie, Leipzig, 1853, p. 264.

In the Muscidæ, on the contrary, each organ of the larva does not become entirely lost, though bordering upon a histolysis, *i. e.* becoming functionally incapable, their histological elements dissolve themselves into a blastema, from which a new histological element must arise. The only difference from the total destruction, such as befalls the muscles, the fat bodies, etc., is this, that the destruction of tissues here becomes a continuous process, and the new organs are built up out of the same material which composed the old ones. This obtains in the intestine, the nervous system and the dorsal vessel. But a surprising analogy to the development of the Echinoderm occurs in the formation of the imaginal disks. As the body of the Echinoderm selects at several points around the alimentary canal of the larva indifferent cell masses, and then all unite and consolidate into a single mass, so arise at different places within the body of the fly larva—here still in genetic relation with the organs of the larva—masses of indifferent cells, which become differentiated in the course of the development of the different parts of the imago, and become transformed into a common whole. It cannot be considered as an essential deviation, that in the Pluteus larva these cell masses are formed during the life of the larva, while in the muscid larva they are formed before that, in the egg; and this deviation occurs to such a slight extent, as we have seen above, that a pair of the formative disks, those out of which the upper half of the prothorax is formed, here makes an exception, and is only developed shortly before the pupation. Had we considered the formation of the cell masses of the Echinoderm larva as buds, then for a still stronger reason is the formation of the imaginal disks of the Muscidæ a budding process. They are outgrowths of the tegumentary membrane of the nerves and tracheæ of tissues, which, if they are not histologically, are yet physiologically equivalents to the complete fibrous tissues of the vertebrates. Both tissues are essentially derived from an amorphous, fundamental substance, which seems to have the capabilities which the more recent studies in histology ascribe to the peculiar restorative quality of the connective tissue of vertebrates, *i. e.* of building up cells, and of returning to that from which it originated.

I find it generally true that the nuclei lying near a recent disk become metamorphosed into disk-forming cells; that they surround themselves with cells, and multiply like the other disk-cells. Such a process may be seen in the exceptionally late appearance of the upper prothoracic disks. These disks are already formed in the egg out of the embryo cells,—out of the same material as the tegumentary membrane with which they develop. They could only in an ideal sense be regarded as outgrowths of this tegumentary membrane; so the upper prothoracic disks are, in reality, nothing but outgrowths. The nuclei of the peritoneal skin form cells, and increase in number, constituting the disks. We have here a bud which scarcely differs from the buds which are concerned in the formation of new stigmata in the first moulting of the larva, and we should almost err in considering the morphological value of this disk to regard it as a true imaginal disk; it should at least not be compared with those of the free Tipulidæ larvæ, in which they have a by far more complicated structure, while they are considerably larger, and are indicated contemporaneously with the formation of the other disks of the thorax.

As I cannot agree with that opinion which regards the well-known metamorphosis of Echinoderms as a metagenesis, so am I still far from proposing that there is such a metamorphosis in the Muscidæ. We must certainly, with V. Carus and J. Müller, consider it in this respect as irrelevant whether the nurse produces one or more germs (in a monogenous way); whether the animal growing from the egg develops into a sexual form, or whether it, not capable of that, at the end of its development produces germs (buds) which build up a sexual animal; or whether the series of developmental forms from the embryo up to the sexually ripe animal end in one or two individuals. The answer in both cases seems to me not doubtful. In the Echinoderms as in the Muscidæ we have to deal with a metamorphosis, not with an alternation of generations. Larva and sexually mature animal are one and the same individual. In the Echinoderms it seems to me this is evident in that the internal organs (intestine and water canal system) are present, and *without any interruption of their functions* pass over from the larval stage to the adult sea star; so that a single germ will not from the beginning pass by gradual differentiation into the perfected animal, but rather distinct accumulations of cells take place and in the course of development give rise to the new "individual."

But in the flies there is another fact which compels us to look upon the larva and pupa as a single individual, however slight may be the community in organs and external form between the two developmental stages. It is this circumstance that the same mass of organized substance constitutes the body of the growing larva, as of the fly. *During the metamorphosis no growth takes place.* The larval skin is thrown off, the insect forms a case around itself beneath whose shelter it remains and builds up the final form of the perfect insect. It takes in or gives out products of combustion of the still unceasing process of respiration. We have in a manner a second egg-development, and as we consider egg and larva as a single individual, so must the pupa, though not containing the undeveloped larva as a yolk, be considered as one and the same individual. But it does not happen that there is no stage in the development of the pupa in which the larval organs are not present; though the organs of flight are indeed newly formed, the exclusion of the larval body does not take place suddenly, but very gradually it grows parallel with a whole series of formations of new structures. Larva and fly overlap each other. There can be no doubt that they are one and the same individual; that their development also is to be considered as a metamorphosis.

It is still the most complete metamorphosis conceivable which we find in the Muscidæ, far more complete — I do not profess to speak from more recent observations — than, for example, the metamorphosis of the Lepidoptera. The destruction of the larval organs is in the Lepidoptera much less complete, as the lepidopterous pupa has the power of moving its hind-body. The muscles of the larval segments concerned in the movements seem to remain, and the nervous power is not interrupted; there is a communication between the nervous centre and the organism; the consciousness of the animal remains, it reacts on stimulation. According to Herold the pulsation of the dorsal vessel goes on. The pupa in short ceases not for a moment to be a living being, while the life of the Muscid is as latent as that of the fertilized egg.

Through the transfer of many organs of the larva into the pupa there is less need of the rebuilding of parts. I find that even in the Lepidoptera *the origin of the thorax is from the hypodermis of the larva;* that no thoracic disks are developed within the body, but that the appendages of the thoracic segments grow by a direct metamorphosis from the limbs. The wings alone have a special mode of development and in a very peculiar way.

I think that the kind and mode of formation of the thorax in the pupa of insects have the closest connection with, at first sight, a very subordinate circumstance, the presence or absence of true limbs in the larva. *I think, that especially where the three segments of the larva immediately following the head bear appendages, the corresponding appendages—the legs—of the adult insect, are formed by a simple metamorphosis; while on the other hand, when these limbs are wanting in the larva, there are found thoracic scales within the body of the larva; and not only the appendages but also the walls of the body are new structures.*

All my observations, new and old, agree with this view; among others the earlier observations on the larva of the gnat, already spoken of, which have only anal limbs, but no typical segmental appendages, and in which the structure of the thorax is the same as in the Muscidæ.

When it is said that the life of the insect is latent in the pupa, that the usual functions of animal life, such as motion and sensibility are wanting, I might speak of the Muscidæ alone, and say this of all insects with a similar mode of formation of the thorax. There comes into consideration here, not only the greater or less independence of development, the more or less marked absence of the larval organs, but also the period of the formation of the pupa. In the Tipulid larva, noticed above, the larval and pupal states are more intimately blended than in the Muscids. The thorax and head of the pupa are already fully formed, while the larva is actively swimming about. When the larva skin is cast off the muscles of the pupa are already at work; the functions of animal life suffer no interruption.

But in the Muscidæ the loss of the larval parts precedes the formation of the body of the pupa. Hence we perceive no motion, and in fact the animal life is latent. The circulation of the blood ceases, the peripheral nervous system is destroyed, and the central system loses any power of action; at the same time all the inner organs become incapable of farther functional conditions. The development of new systems of organs begins with the rise of indifferent cells in the mass to be sloughed off, much as happens in the formation of the blastoderm in the egg. This renewal of the structure is seen in a measure in the internal organs. We can distinguish four modes of development, according to which the parts of the fly originate. Either certain parts of the larvæ become persistent, under modification, or the larval organs become a foundation for the parts of a fly, but are thrown off, cell by cell, ere they assume a definite character. The third and last kind is when an entirely new development of parts takes place, the beginning of which either dates at the embryonic or larval period or at the close of the pupa state.

Let us consider this single mode of development more closely as regards the direct transfer of the larval parts alone from the hypodermis of the eight hinder larval segments, which are afterwards developed into the abdomen of the fly. The second mode occurs in the alimentary canal, the Malpighian vessels, with the dorsal vessel and the central part of the nervous system. The same process is observed in all these organs, that of their removal, cell by cell, with a succeeding new development. I might term it a *histolysis*. The histological elements of the organ—simple as well as compound—suffer a fatty degeneration; there remains a residuary mass filled mostly with fat molecules. In the nervous centres and Malpighian vessels the nuclei of the cells become persistent, and perhaps give rise to the development of new histological elements; whether this persistent mass deports itself like the alimentary canal, or whether after its destruction it retains the nuclei, must remain undetermined, nevertheless this same mass, which had composed the former organs, serves to build up anew the new ones. The products resulting from this destruction of organs are not wholly dispersed, but remain together and so receive the form of organs in their totality, even if no single histological element remain.

We must here leave undetermined how the cells which are to form the new organs originate, though this cannot be doubtful as regards the last two modes of development of the parts of the imago. They undergo a completely new development, *i. e.* of all those parts which are not generally present in the larva, or are not in their complete state of functional activity. In this last category belongs the thorax *and head of the fly and their appendages*, also those parts of the imago which arise from the disks;

also the *genital glands.* With a single exception all these parts are already formed in the egg, their cells also arise directly from the cells of the embryo, and in the upper prothoracic disks, which are afterwards formed, there is still a continuity between the embryonal cells and those of the disks if still indirect, through the mediation of the nuclei of the peritoneal membrane surrounding the tracheæ.

It is well to remark—and it is based on a grand plan in the development of the imago—that only the walls of the parts referred to arise from the formative disks, the skin alone and not the muscles. These last owe their origin to a new process of cell formation which generally obtains in the last half of the period of pupation, and gives the material for the development of the inner organs still wanting, the tracheæ, nerves, the fat body of the fly, and the genital armature. I have sought to call attention to the fact that we are dealing with a "free" cell formation, *i. e.*, that the newly formed cells arise directly or indirectly from cells. In the early part of these researches it was proved that the first cells in the fertilized egg show a process of free cell formation, arising independently from some previous formative element. An objection to this could be raised, that we have to do with an endogenous cell growth, while the whole egg should be considered as a cell. It is clearly shown to be in agreement with the earlier observations of Stein and Lubbock, that the insect egg is not the equivalent of a single cell, but is composed of a number of cells. Should this objection be laid aside, then a similar objection in the cell growth of the inner parts of the pupa could not arise, and if the relation be proved by fresh observations, then there may be a free cell growth in the living organism.

ENGLISH SPARROWS.

BY THOMAS G. GENTRY.

In the September issue of the NATURALIST, Dr. Brewer reviews at considerable length a small article which appeared in a previous number, from the pen of Dr. Coues, concerning the European